
Modelling Trends in *Powelliphanta patrickensis* Snail Populations on Buller Plateaux

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EXECUTIVE SUMMARY

Results from monitoring populations of *Powelliphanta patrickensis* snails in two capture-recapture plots on Denniston Plateau over the nine-year period 2014–2024 and from surveys of more than one-hundred 10 m square plots spread throughout the species' distribution range on Buller Plateaux during 2012 and 2024 show that there has been a 60% decline in the species population on Buller Plateaux since 2012. Evidence from shells collected during the 2012 and 2024 surveys indicate that the population decline was primarily a result of increased predation by weka (*Gallirallus australis*), a native rail. 35% of 388 shells collected in 2024 showed evidence of predation by weka, compared to 6% of 658 shells in 2012. Evidence of rat predation was found on 6% of shells found in 2012 and 16% of shells found in 2024.

Information from these two investigations was used to develop models of likely long-term trends in populations of *P. patrickensis* with the observed levels of predation by weka, rodents and possums, and populations without predation by them.

A number of models were developed using a range of likely demographic parameter estimates obtained from the capture-recapture study. In models with predation by weka and rodents, the snail population declined by 89% (Range 68%–96%) after 20 years and by 96% (Range 82%–99%) after 30 years. In all models without predation by weka, rodents and possums, populations of *P. patrickensis* increased rapidly towards whichever carrying capacity was used in the model with the time taken to reach carrying capacity depending on the combination of demographic parameters used in the models. Typically, populations without predation by weka, rodents or possums approached carrying capacity within 30 years.

Bathurst Resources Ltd. is proposing the Buller Plateaux Continuation Project (the “Project”) to extend the life of Stockton Mine on Buller Plateaux (i.e., Stockton and Denniston Plateaux). The Project will reduce the current distribution range of *P. patrickensis* by 4.58 km² (i.e., 22.3% of 20.52 km²) on Dennison Plateau and 1.95 km² (i.e., 6.1% of 32.01 km²) on Stockton Plateau. To compensate for the project's residual impacts on *P. patrickensis* snails, Bathurst Resources is proposing the creation of 4 pest-free fenced exclosures on Buller Plateaux to halt predation of *Powelliphanta* snails by weka, rodents and possums. There will be two exclosures to protect *P. patrickensis* on Denniston Plateau: a 0.473 km² (47.3 ha) exclosure, completed one year after mining commences, and a 1.543 km² (154.3 ha) exclosure, completed 4 years after mining commences. On Stockton Plateau, there will be a 6.945 km² (694.5 ha) exclosure to protect *P. patrickensis* completed 9 years after mining commences, but only 5.44 km² (544.0 ha) of the exclosure is in the known range of *P. patrickensis*. There will also be a 0.014 km² (14.6 ha) exclosure to protect *P. augusta*. When areas of snail habitat are to be disturbed, wherever possible the intact habitat will be transferred using vegetation direct transfer (VDT). Where VDT cannot be used areas will be searched for snails before stripping of snail habitat commences and any snails found will be relocated to a nearby pest-free exclosure or, when completed pest-free exclosures are not available, they will be relocated to a nearby area that will eventually be in a pest-free exclosure. Models of the effects of disturbance caused by the Project and associated effects management and compensation package on snail populations on the two plateaux were developed by combining models of trends in *P. patrickensis* snail

populations with and without predation with the schedules of mining disturbance in the Project mine plan and the proposed construction schedule for pest-free fenced exclosures. Models of snail population trends with the Project were compared to population trends without the project assuming the current predation levels.

In models of the snail populations with the Project and the proposed pest-free exclosures, there were initial reductions in the size of the snail populations as a result of stripping snail habitat and continued predation outside the pest-free exclosures, but as snail populations in the pest-free exclosures begin to grow, in the absence of predation by weka, rodents or possums, population declines on both plateaux slowed and snail populations in models with and without the Project were similar after between 9 and 11 years. Subsequently, in models with the Project, populations either leveled out or increased as they approached the carrying capacity of the pest-free exclosures, usually within 30 years.

Because of the complexity and unpredictability of the real world, it is unrealistic to expect that the population models described in this report will provide accurate descriptions of future trends in *P. patrickensis* snail populations on Buller Plateaux. However, the models provide useful insights into the likely fates of the snail populations with and without the Project.

Although there was no attempt to incorporate the effects of climate change on *P. patrickensis* populations in the models, because of lack of reliable information, the predicted impacts of climate change on *P. patrickensis* are desiccation caused by increased soil moisture deficits and increased predation by increased rat abundance. Desiccation will affect snail populations with and without the Project similarly, whereas increased predation by rats will only affect snails outside of the pest-free exclosures. Consequently, negative effects of climate change on *P. patrickensis* population trends will be larger without the Project and proposed pest-free exclosures.

Although, stripping of snail habitat for the proposed Project will result in considerable reductions in the area of available habitat for *P. patrickensis* on Buller Plateaux and initial reductions in population size, the models show that the pest-free exclosures proposed as compensation for the Project's residual impacts on snails will reverse ongoing declines in *P. patrickensis* populations on the two plateaux caused by predation and result in stable, viable snail populations, within 30 years, albeit with lower numbers of snails than are currently present, primarily because of the impact of predation outside of the pest-free areas.

INTRODUCTION

Background

Results from monitoring populations of *Powelliphanta patrickensis* snails in two 70 m square capture-recapture plots on Denniston Plateau over the nine-year period 2014–2024 (Lloyd, 2024a) and from surveys using diurnal sub-surface searches of two-hundred and twenty-four 10 m square plots spread throughout the species’ distribution range on Buller Plateaux during 2012 and one-hundred and twenty-three 10 m square plots during 2024 (Lloyd, 2024b) show that there have been large declines in the species’ abundance on Buller Plateaux since 2012. Density estimates for snails in the two capture-recapture plots declined by 62% between summers 2014–15 and 2023–2024. Results from the surveys of 10 m square plots were similar, with a 59% population decline between surveys in 2012 and 2024.

Because most snails < 20 mm were not tagged during capture-recapture surveys, only records from snails with maximum diameter ≥ 20 mm were included in capture-recapture analyses. Consequently, population estimates, and demographic parameter estimates from capture-recapture analyses are for snails with maximum diameter ≥ 20 mm.

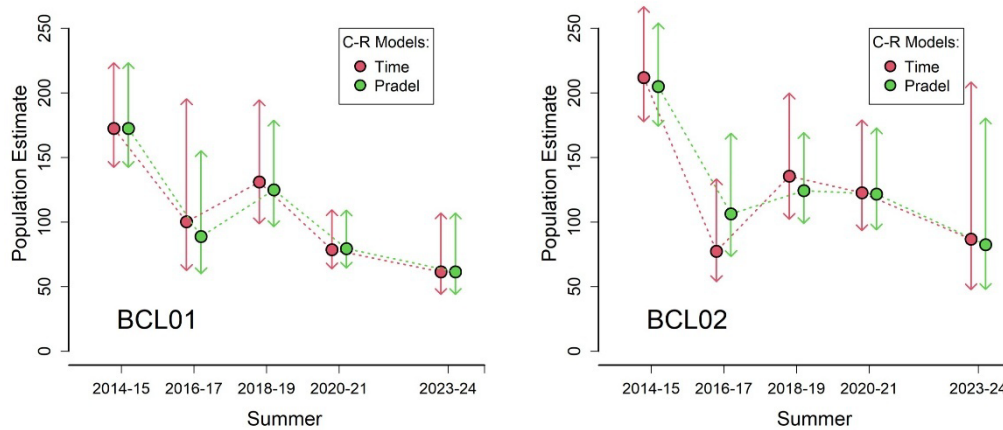


Figure 1. (From Lloyd 2024a). Population estimates for *P. patrickensis* in two capture-recapture plots (BCL01 & BCL02) during the period 2014 to 2024. There are two population estimates for each survey. The “Time” estimates are from Huggin’s closed population analyses using time-only models and the “Pradel” estimates are from Pradel’s robust design model.

Throughout the nine-year monitoring period, snail population trends in the two plots showed very similar patterns (Figure 1 and Table 1). Population density estimates from the two capture-recapture plots combined declined by 61.7% (CI95%: 43% – 80%) from 385.0 (CI95%: 328 – 441) snails⁻¹ ha in summer 2014–15 to 146.7 (CI95%: 78.9 – 213) snails⁻¹ ha in summer 2023–24. Although the population trend varied between intervals, with the largest decline occurring between summer 2014–15 and 2016–17, the long-term trend was consistent decline.

Table 1. (From Lloyd 2024a). Population estimates with standard errors (SE) and 95% confidence intervals (CI95%) from Pradel's robust design model for *P. patrickensis* in two capture-recapture plots (BCL01 & BCL02) on Denniston Plateau during the period 2014 to 2024.

Summer	Plot Population Estimates					
	Plot BCL01			Plot BCL02		
	Est	SE	CI95%	Est	SE	CI95%
2014–15	172.4	20.1	(142 – 223)	204.9	19.9	(174 – 254)
2016–17	88.8	22.7	(60 – 155)	106.2	23.3	(73 – 168)
2018–19	124.8	20.1	(96 – 179)	124.3	17.3	(99 – 169)
2020–21	79.2	10.8	(64 – 109)	121.5	19.3	(94 – 173)
2023–24	61.4	14.7	(44 – 107)	82.3	30.5	(48 – 180)

Evidence from shells collected during the 2012 and 2024 diurnal surveys of 10 m square plots (Table 2) indicate that the population decline was primarily a result of increased predation by weka (*Gallirallus australis*), a native rail. The proportion of snail shells found with evidence of predation by weka increased from 6% of 658 shells found during diurnal sub-surface searches of 224 plots in 2012 to 35% of 388 shells found during searches of 123 plots in 2024 (Lloyd, 2024b). Although the proportion of shells with evidence of rat predation increased from 6% in 2012 to 16% in 2024, the results of a multiway GLM with environmental variables showed that the increase in the proportion of shells with rat damage was not a result of increased in rat predation, but because a greater proportions of plots with vegetation types where rat damage was common were surveyed during 2024 than 2012 (Lloyd, 2024b).

Table 2. Numbers and proportions of damage patterns assigned to 388 shells with identifiable patterns examined during plot surveys in 2024 (Lloyd, 2024b). CI95% is the 95% confidence intervals around the estimated proportion.

<u>Mortality Type</u>	N.	Prop.	SE	(CI95%)
Shell State				
Natural mortality:				
Intact	136	0.351	0.024	(0.30 – 0.40)
Bird	4	0.010	0.005	(0.00 – 0.06)
Trampled	22	0.057	0.012	(0.01 – 0.11)
Total natural mortality:	162	0.418	0.025	(0.37 – 0.47)
Preyed on:				
Weka	136	0.351	0.024	(0.30 – 0.40)
Rat	64	0.165	0.019	(0.11 – 0.22)
Mouse	15	0.039	0.010	(0.00 – 0.09)
Possum	11	0.028	0.008	(0.00 – 0.08)
Total preyed on mortality	226	0.582	0.025	(0.53 – 0.63)

Buller Plateaux Continuation Project

The Buller Plateaux Continuation Project (the “Project”) proposed by Bathurst Resources Ltd. is designed to extend the life of Stockton Mine on Buller Plateaux. Construction for the Project will reduce the current distribution range of *P. patrickensis* by 4.58 km² (22.3% of 20.52 km²) on Denniston Plateau and 1.95 km² (6.1% of 32.01 km²) on Stockton Plateau (Table 3).

Table 3. Areas in the distribution ranges of *P. patrickensis* on Stockton and Denniston plateaux affected by the proposed opencast mining, from Lloyd's Ecological Consulting (2026).

Plateau:	Area (km ²)		Proportion to be Disturbed
	Current Distribution	Proposed Disturbance	
Denniston	20.52	4.58	22.3%
Stockton	32.01	1.95	6.1%

Bathurst Resources Ltd. are proposing a programme of effects management to mitigate the impact of the Project on *P. patrickensis*. During excavations and earthworks undertaken for the Project, snail mortality and snail habitat loss will be minimised by using Vegetation Direct Transfer (VDT) wherever possible. VDT entails stripping overburden as slabs of topsoil with intact native vegetation and transferring the slabs to a prepared site where they are reassembled. Recent studies show most snails survive in habitat transferred by VDT, with viable populations remaining 13 years after VDT (Gruner et al., 2021; Lloyd, 2021, 2023, 2024c; MacKenzie, 2014; MacKenzie, 2020). Where VDT cannot be used during habitat stripping because of engineering and practical constraints, including scheduling and availability of suitable landforms, snail mortality will be minimised by salvaging snails. Snail salvage will entail relocating snails from disturbance areas before habitat is stripped to areas not scheduled for disturbance, ideally fenced pest-free exclosures. To compensate for the Project’s residual impacts on *P. patrickensis* snails and their habitat Bathurst Resources are also proposing creation of several pest-free fenced exclosures in areas of *P. patrickensis* habitat. The exclosures are primarily designed to halt weka predation, the main cause of recent declines in *P. patrickensis* populations on Buller Plateaux, but will also exclude rodents and possums.

During previous snail salvage operations, daytime sub-surface searches were used to find snails and snail eggs for translocation. Comparison of results from recent capture-recapture surveys (Lloyd, 2024a) using nocturnal searches to find snails active on the surface and results from surveys using daytime sub-surface searches of 10 m square snail plots (Lloyd, 2024b) demonstrate that nocturnal searching is considerably more cost-effective than daytime searching. Average capture rates for the two methods were 0.75 person-hours per snail during nocturnal searches and 9.1 person-hours per snail during daytime searches. Although daytime searches are likely to find higher proportions of snails present in search areas (18% v. 11%), daytime searches require 400 person-hours to search one hectare compared to 11.4 person-hours for nocturnal searches. Another advantage of nocturnal searching compared to daytime searching is that a higher proportion of the snails caught at night are reproductively mature.

In mine plans, VDT will be used to rehabilitate at least 15 % of the areas of snail habitat being stripped for the Project on the two plateaux. The proportions of snails found during salvage

operations are difficult to predict, but during nocturnal searches of the 0.49-hectare capture-recapture plots, the mean proportion of snails (≥ 20 mm diameter) present in the plots captured during each search was 11.3%, with a range of 8.7%–14.7% (Lloyd, 2024a). Thus, it is reasonable to expect that 10% of snails ≥ 20 mm diameter present in areas being stripped without rehabilitation by VDT will be found and salvaged during a single nocturnal search of an area, with suitable conditions. Snails < 20 mm diameter are also found during nocturnal searches, but there is insufficient information to estimate the proportion likely to be found.

Planning for fenced pest-free exclosures to protect *P. patrickensis* from predation by weka, rodents and possums is underway, with the most recent plans (Figure 2) including two exclosures (47.3 ha and 154.3 ha) on Denniston Plateau, and a 694.5-ha exclosure on Stockton Plateau, which will include 544.0 ha of undisturbed *P. patrickensis* snail habitat. Another 14-ha exclosure will be established on Stockton Plateau to protect *P. augusta* from predation. Information from demographic studies on *P. patrickensis* (Lloyd, 2024a, 2024b) was used to develop models to predict trends in the *P. patrickensis* population on Buller Plateaux with and without the impact of the proposed mine Project and the proposed effects management and compensation.

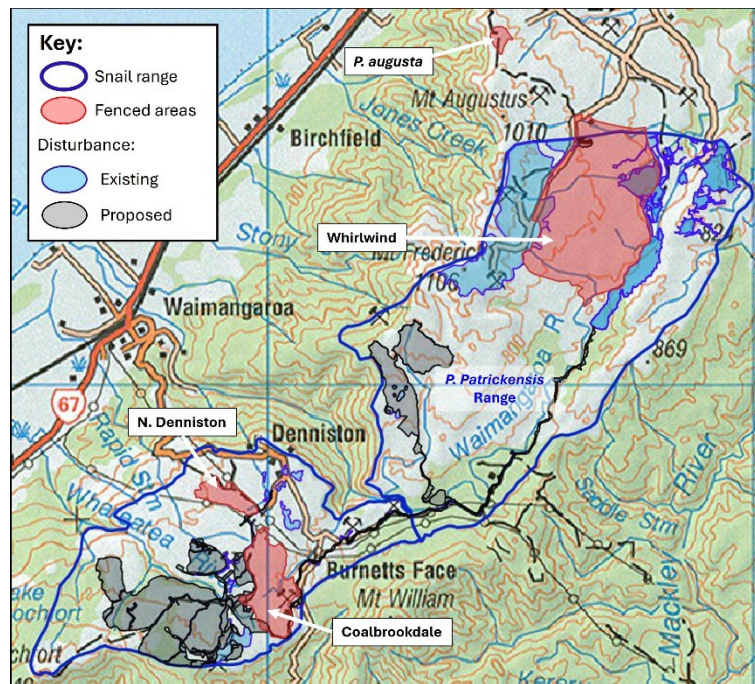


Figure 2. Map of fenced pest-free exclosures proposed to compensate for impacts of the Project.

METHODS

Modelling Future Population Trends

Two methods were used to model future trends in *P. patrickensis* populations: a simple exponential model for density-independent population change (Williams et al., 2001) and a logistic model of density-dependent population growth in discrete time intervals (Williams et al., 2001).

In the exponential model (Equation 1), N_t and N_{t+1} are population sizes at years t and $t+1$ respectively and λ is the annual finite rate of population increase. The population size changes by a factor of λ for each unit time, with the rate of population change not affected by population density. The exponential model was used to model declining populations where λ is less than one and it can be assumed that decline rate is not affected by population density.

$$\text{Equation 1: } N_{t+1} = N_t \lambda$$

In the logistic model of density-dependent population growth (Equation 2), growth rate declines as population density increases to the local carrying capacity K (i.e., the maximum population density).

$$\text{Equation 2: } N_{t+1} = N_t + N_t(\lambda - 1) \left(1 - \frac{N_t}{K}\right)$$

Population trends over thirty-year periods were obtained from the two models by recursive implementation of Equations 1 & 2 from $t = 0$ to $t = 30$.

Parameter Estimates for Variables with Non-normal Distributions

Demographic parameter estimates used in models of snail population trends have non-normal distributions. Fecundity, annual finite rate of population increase and population abundance are best described by log-normal distributions (Limpert et al., 2001), while survival, mortality and proportion are random variables with values between 0 and 1, which are best described by the beta distribution (Thompson Hobbs & Hooten, 2015). Error propagation and bootstrapping procedures used to develop the population models require parameter estimates for the appropriate distributions derived from the mean and variance or standard deviation of the original variables as described in Appendix 1.

Deriving Estimates of Lambda With Predators (λ_{pred})

To estimate λ , the annual finite rate of population increase, in the presence of all snail predators present on Buller Plateaux (λ_{pred}), including weka, rodents and possums, I used estimates of snail population densities (ha^{-1}) obtained from capture-recapture surveys during 2014–15 and 2023–24 ($N_{2014} = 385$ and $N_{2023} = 147$) and the length of the intervals between the two surveys ($Yrs = 9$) in Equation 3.

$$\text{Equation 3: } \lambda_{pred} = \left(\frac{N_{2023}}{N_{2014}} \right)^{(1/Yrs)}$$

Snail population densities and lambda estimates are likely to have log-normal distributions, therefore, to get standard deviations and confidence intervals around the estimated λ_{pred_x} , I used Equations 10 a & b in Appendix 1 to obtain estimates of the location and dispersion parameters (α and β) for the log-normal distribution from the means and standard errors of the population density estimates, i.e., $N_{t_x}(\mu, \sigma) \rightarrow N_{t_y}(\alpha, \beta)$, and then used Equation 4, the logarithmic form of Equation 3, to obtain estimates of the mean and standard deviation for λ_{pred_y} using the R-function *propagate* for error propagation.

$$\text{Equation 4: } \lambda_{pred_y} = (N_{2023_y} - N_{2014_y})/Yrs$$

The mean and standard deviation for λ_{pred_x} were obtained from the location and dispersion parameters for λ_{pred_y} , i.e., $\lambda_{pred_y}(\alpha, \beta) \rightarrow \lambda_{pred_x}(\mu, \sigma)$, using Equations 11 a & b in Appendix 1. The 95% confidence interval (CI_x) around the mean of λ_{pred_x} was calculated using Equation 12 a & b in Appendix 1.

Estimating Survival, Fecundity & Lambda Without Predators (S_{nat} , f_{nat} & λ_{nat})

Partitioning Mortality Rates

Predicting *P. patrickensis* population trends in the proposed pest-free fenced exclosures requires estimates of mortality and fecundity in the absence of the predator species that will be excluded from the fenced exclosures (i.e., weka, rodents and possums).

To partition mortality caused by the predator species to be excluded from the exclosures and mortality from other causes, I used information on the probable cause of damage on 410 shells collected during daytime searches of 123 ten-metre square plots spread throughout Buller Plateaux in 2024 (Lloyd, 2024c), with probable cause of shell damage determined using criteria based on Meads, Walker, and Elliott (1984). Most (58%) of the 388 shells examined and in good enough condition for damage patterns to be recognized showed evidence of predation by one of the predators that will be excluded from the fenced exclosures (Table 2).

Separate rates were estimated for mortality caused by weka, rodents or possums (m_{pred}) and for mortality caused by other factors (m_{nat}) for each interval between plot surveys using Equations 5 and 6, where S_{obs} is observed survival between plot surveys, P_{pred} is the proportion of shells with evidence of predation by weka, rodents or possums and P_{nat} is the proportion of shells without evidence of predation by predators.

$$\text{Equation 5: } m_{pred} = P_{pred}(1 - S_{obs}) / (1 - P_{nat}(1 - S_{obs}))$$

$$\text{Equation 6: } m_{nat} = P_{nat}(1 - S_{obs}) / (1 - P_{pred}(1 - S_{obs}))$$

Estimates of m_{nat} were then used to estimate likely snail survival rates in the absence of weka and rodents (S_{nat}) using $S_{nat} = 1 - m_{nat}$. The R-function *propagate* was used to obtain standard deviation and CI95% around each of the estimates.

Fecundity Estimates

Snails < 20 mm diameter were not tagged during the capture-recapture programme, consequently observed annual fecundity is per capita recruitment rate of snails with diameters ≥ 20 mm per snail in the population at the start of the interval. Thus, estimates of fecundity from the capture-recapture surveys (f_{obs}) include both productivity and survival for the life stage from eggs to 20 mm diameters snails, which takes *c.* 2 years.

Fecundity estimates from the capture-recapture surveys (f_{obs}) were converted to estimates of fecundity per capita mature snails f_m by dividing f_{obs} for each plot survey by the proportion of mature snail (i.e., ≥ 30 mm diameter) present on the plot at the beginning of the interval between surveys.

Estimates of fecundity in the absence of weka and rodent predation (f_{nat}) were obtained from estimates of S_{obs} , S_{nat} and f_m using Equation 7, which adjusts f_m for the difference in annual survival over the two-year period between eggs being laid and snails reaching 20 mm diameter.

$$\text{Equation 7: } f_{nat} = f_m \left((S_{nat})^2 / (S_{obs})^2 \right)$$

The R-function *propagate* was used to obtain standard deviation and 95% confidence intervals (CI95%) around each of the fecundity estimates.

Bootstrapping

Bootstrapping was used to obtain confidence intervals around demographic parameter estimates obtained using Equations 5–7 described above and Lefkovitch matrices (Lefkovitch, 1965) to estimate population growth rates (Appendix 2).

Weighted Means of Survival and Fecundity

Weighted means of the parameters of observed survival in the presence of predators (S_{obs}) and fecundity per capita of mature snails (f_m) during the capture-recapture monitoring programme were calculated using the length, in years, of the 8 intervals between successive surveys of the two plots (D_t) as weighting (Equation 8).

$$\text{Equation 8: } \text{Weighted Mean} = \sum_{t=1}^n Par_t \times D_t / \sum_{t=1}^n D_t$$

The R-function *propagate* was used to estimate standard deviations and CI95% for the weighted means of the parameters S_{obs} , and f_m , with conversion of the mean and standard deviation to and from parameters for the non-normal distributions as described in Appendix 1.

Mortality with and without predators, and survival without predators

Equations 13 a & b in Appendix 1 were used to obtain beta parameters (θ and δ) from the weighted means of observed annual survival rate (S_{obs}) and the proportions of shells preyed on (P_{pred}) and not preyed on (P_{nat}) by weka, rodents or possums. The beta parameters were used in the R-function *rbeta* to generate 1000 random deviates for each of the three variables. Estimates of mortality rates with and without predators (m_{pred_i} and m_{nat_i}) were obtained for each of the 1000 sets of the three random deviates using Equations 5 & 6. Estimates of annual survival in the absence of weka, rodents and possums (S_{nat_i}) were obtained for each of the 1000 estimates of m_{nat_i} using $S_{nat_i} = 1 - m_{nat_i}$.

Fecundity without predators

Equations 10 a & b in Appendix 1 were used to obtain estimates of the log-normal parameters from the weighted means and standard deviation of fecundity per capita of mature snails (f_m). The log-normal distribution parameters for f_m were then used in the R-function *rlnorm* to generate 1000 random deviates. Each of the 1000 random deviates of f_{m_i} were combined with each of the 1000 sets of random variates for S_{pred_i} and S_{nat_i} obtained previously to create 1,000,000 sets of S_{pred_i} , S_{nat_i} and f_{m_i} that were used in Equation 7 to obtain 1,000,000 estimates of f_{nat_i} .

Obtaining Estimates of Lambda from Lekovitch Matrices

Lefkovitch's stage-structured population projection matrix model (Lefkovitch, 1965), described in Appendix 2, was used to derive an estimate of lambda in the absence of weka and rodents (λ_{nat_i}) from each of the 1,000,000 sets of randomly generated values for survival and fecundity in the absence of weka and rodents (S_{nat_i} and f_{nat_i}). Summary statistics (mean, standard deviation, and 25% and 97.5% quantiles) were obtained for the 1,000,000 values of S_{pred_i} , S_{nat_i} , f_{pred_i} , f_{nat_i} and λ_{nat_i} . To obtain 95% confidence intervals for λ_{nat} , Equations 10 a & b in Appendix 1 were used to obtain estimates of the log-normal distribution parameters for λ_{nat} from the mean and standard deviation of λ_{nat} . Equations 11 & 12, a & b, in Appendix 1 were then used to get the mean, standard error and 95% confidence interval for λ_{nat} .

Using Lambda (λ) Estimates to Model Population Trends

Models of population trends over a 30-year period were obtained by recursive implementation of exponential and logistic population models (Equations 1 & 2) from $t = 0$ to $t = 30$ using estimates of λ_{pred} & λ_{nat} respectively. The exponential model for density-independent population change (Equation 1) was used for populations with $\lambda < 1$ (i.e., λ_{pred}) while the logistic model of density-dependent population growth (Equation 2) for populations with $\lambda \geq 1$ (i.e., λ_{nat}). To investigate the influence of population carrying capacity on population trends from the logistic model of density-dependent population growth, two estimates of carrying capacity (K) were used: a low value of 385 snails⁻¹ ha (K_{lo}), based on the observed population density during summer 2013–14, and a 50% higher value of 578 snails⁻¹ ha (K_{hi}).

To ensure that N_t didn't reach zero during recursive implementation, an initial population size (i.e., N_0) of 1000 was used instead of the current population density of 146.7 snails⁻¹ ha.

Consequently, for population projections with $N_0 = 1000$, values of the two carrying capacity estimates (K_{lo} & K_{hi}), were scaled up to 2,624 and 3,936 respectively.

Two methods were used to create confidence intervals around the expected population trends. In one method the 2.5% and 97.5% quantile estimates for λ_{pred} and λ_{nat} were used to model the lower and upper 95% confidence limits for population trends using recursive implementation of Equations 1 & 2. In a second method, the R-function *propagate* was used for recursive implementation of logarithmic forms of the exponential and logistic population models described below.

Recursive implementation of a logarithmic form of the exponential model

To prepare for recursive implementation of a logarithmic form of the exponential model (Equation 9), log-normal population parameters for λ_{pred} , λ_{nat} and N_t were obtained from their means and standard deviations, i.e., $\lambda_x(\mu, \sigma) \rightarrow \lambda_y(\alpha, \beta)$ and $N_{t,x}(\mu, \sigma) \rightarrow N_{t,y}(\alpha, \beta)$, using Equations 10 a & b in Appendix 1. The R-function *propagate* was then used for recursive implementation of the logarithmic form of the exponential model (Equation 9) to generate population values $N_{t,y}$ from $t = 0$ to $t = 30$, with the means and standard errors for each estimate of $N_{t,y}$.

$$\text{Equation 9: } N_{(t+1),y}(\alpha, \beta) = N_{t,y}(\alpha_{t,y}, \beta_{t,y}) + \lambda_y(\alpha, \beta)$$

The means, standard deviations and 95% confidence intervals for population sizes ($N_{t,x}$) from $t = 0$ to $t = 30$ were then obtained from the means and standard errors for $N_{t,y}$ using Equations 11 a & b in Appendix 1, i.e., $N_{t,y}(\alpha, \beta) \rightarrow N_{t,x}(\mu, \sigma)$.

Recursive implementation of a logarithmic form of the logistic model

Recursive implementation of logarithmic forms of the logistic model for density-dependent population growth proved more complex, entailing repeated conversion between mean and standard deviations of variables and the parameters of their distributions as well as two separate logarithmic mathematical operations undertaken using the R-function *propagate*.

Implementing the logarithmic form of the logistic model begins with converting the mean and standard deviation of $(\lambda - 1)$ from the log-normal distribution using Equations 10 a & b in Appendix 1, i.e., $\lambda_x(\mu, \sigma) - 1 \rightarrow r_y(\alpha, \beta)$. Subsequently, each implementation of the logarithmic form of the logistic model from $t = 0$ to $t = 30$ required the following steps:

Step1: Convert the mean & standard deviation of $N_{t,x}$ to log-normal parameters using Equations 10 a & b in Appendix 1, i.e., $N_{t,x}(\mu, \sigma) \rightarrow N_{t,y}(\alpha, \beta)$ & $N_{t,x}(\mu, \sigma)/K \rightarrow NK_{t,y}(\alpha, \beta)$.

Step2: Propagate the logarithmic expression:

$$\Delta_{t,y}(\alpha, \beta) = r_y(\alpha, \beta) + NK_{t,y}(\alpha, \beta).$$

Step2: Convert log-normal parameters for $\Delta_{t,y}$ to mean and standard deviation using Equations 11 a & b in Appendix 1, i.e., $\Delta_{t,y}(\alpha, \beta) \rightarrow \Delta_{t,x}(\mu, \sigma)$.

Step 3: Convert the mean and standard deviations for $1 + \Delta_{t,x}$ to log-normal parameters using Equations 10 a & b in Appendix 1, i.e., $\Delta 1_{t,y}(\alpha, \beta) = 1 + \Delta_{t,x}(\mu, \sigma)$.

Step 4: Propagate the logarithmic expression:

$$N_{(t+1)_y}(\alpha, \beta) = N_{t_y}(\alpha, \beta) + \Delta_{t_y}(\alpha, \beta).$$

Step5: Convert log-normal parameters for N_{t+1} to mean and standard deviation using Equations 11 a & b in Appendix 1 and get the confidence interval around the log-normal mean using Equations 3 a & b, i.e., $N_{t_y}(\alpha, \beta, CI) \rightarrow N_{t_x}(\mu, \sigma, CI)$.

Modelling Population Trends With and Without the Project

To model snail population trends without the Project and snail population trends in areas outside of the fenced pest-free areas with the Project, the exponential model (Equation 1) was used with estimated mean, and upper and lower confidence intervals for λ_{pred} , the annual finite rate of population increase, in the presence of all snail predators present on Buller Plateaux (including weka, rodents and possums).

To model snail population trends inside the fenced pest-free areas with the Project, the logistic model (Equation 2) was used with estimated mean, and upper and lower confidence intervals for λ_{nat} , the annual finite rate of population increase, without snail predators excluded from the fenced pest-free areas (i.e., weka, rodents and possums). Two estimates of carrying capacity were used in the logistic model a low value of 385 snails⁻¹ ha (K_{lo}), based on the observed population density during summer 2013–14, and a 50% higher value of 578 snails⁻¹ ha (K_{hi}).

Population trends on the two plateaux were modelled separately. All models began with an initial population density of 146.7 snails⁻¹ ha, the estimated population density on Denniston Plateau during summer 2023–24. The total number of snails at the start of the models was calculated by multiplying snail density by distribution range areas (i.e., 2,052 ha and 3,201 ha on Denniston and Stockton Plateau respectively).

Modelling population trends with the Project required concurrent exponential and logistic models for snails in areas outside and within the pest-free fenced areas respectively. At each yearly iteration of models of the Project, information in Table 4 on the areas of snail habitat disturbed, rehabilitated by VDT and searched for snails during the year together with the area of pest-free fenced exclosures available was used to adjust the numbers of snails entering the exponential and logistic population models respectively.

Model Assumptions

Models of likely snail population trends on Buller Plateaux with and without the Project were based on a number of assumptions:

1. Without altered conservation management intervention, the observed declines in snail populations on the two plateaux between surveys in 2012 and 2024 and during repeated surveys of capture-recapture plots during the 2014–2024 period (Lloyd, 2024a) would continue unabated outside of pest-free exclosures. Consequently, population trends

outside of pest-free exclosures can be modelled using λ estimates for populations with predation by weka, rodents and possums (i.e., λ_{pred}).

2. Snails placed in the pest-free exclosure areas would not be subject to predation by weka, rodents or possums. Consequently, population trends in pest-free exclosures can be modelled using λ estimates for populations without predation (i.e., λ_{nat}).
3. Snails in areas rehabilitated by VDT would survive the VDT process, but would remain vulnerable to predation by weka, rodents or possums. Construction of temporary weka-proof fences around areas of VDT is being considered, but is not included in the models.
4. Before an area is stripped for mining, there will be a single nocturnal search of the area to find and relocate snails. Results from capture-recapture surveys indicate that 10% of the snails ≥ 20 mm diameter present in an area will be found and salvaged during a single nocturnal search before areas are stripped, with 11.4 person hours required to search one hectare.
5. Salvaged snails will be relocated to a pest-free fenced area if available, or when completed pest-free exclosures are not available, salvaged snails will be relocated to locations that will eventually be inside pest-free fenced areas.
6. Two pest-free fenced areas will be established on Denniston Plateau: a 47.3 ha fenced area completed one year after mining commences, and a 154.3 ha fenced area completed 4 years after mining commences.
7. A single 694.5 ha pest-free fenced areas will be established on Stockton Plateau, with 661.8 ha of the area in the known distribution range of *P. patrickensis*, but only 544.0 ha in undisturbed *P. patrickensis* snail habitat. The fenced area on Stockton Plateau will be completed 9 years after mining commences on the Stockton Plateau.
8. A schedule of the areas of snail habitat to be disturbed during each year of the Project prepared during March 2025 (Table 4) was obtained from the Mine Plans and used to model changes in the snail populations on the two plateaux during the Project. Changes to the schedule since March 2025 will be minor and have little effect on the results.

Table 4. Schedule of areas (ha) of snail habitat to be disturbed, rehabilitated by VDT and searched for snails (i.e. salvaged) during each year of the project.

Project Year	Denniston			Stockton		
	Disturbed	VDT	Salvaged	Disturbed	VDT	Salvaged
0	0.0	0.0	0.0	0.0	0.0	41.7
1	0.0	0.0	105.1	41.7	0.0	7.2
2	109.7	4.6	62.8	13.1	5.9	7.6
3	77.4	14.6	111.5	11.2	3.7	6.3
4	121.2	9.7	11.8	7.7	1.4	7.4
5	18.4	6.6	18.6	8.8	1.4	2.7
6	33.0	14.4	0.0	3.5	0.8	9.2
7	0.0	0.0	22.9	9.9	0.7	27.3
8	25.6	2.7	0.0	29.9	2.6	5.1
9	0.0	0.0	7.4	7.6	2.5	10.5
10	12.9	5.5	17.8	14.7	4.3	14.7
11	24.0	6.3	25.1	19.0	4.3	4.0
12	28.7	3.6	3.9	4.6	0.6	18.5
13	4.6	0.7	2.9	19.4	0.9	3.3
14	2.9	0.0	0.0	3.5	0.2	0.3
15	0.0	0.0	0.0	0.3	0.0	0.0

RESULTS

Estimates of Demographic Parameters

Estimates of Lambda With Predators (λ_{pred})

The estimated annual finite rate of population change in the presence of all the snail predators present on Denniston Plateaux (λ_{pred}) during the 9-year period 2014 to 2023 is 0.896 (SD: 0.024; CI95%: 0.850–0.945). This value of λ_{pred} will result in the snail population declining by 10% annually.

The weighted mean for annual survival rate (S_{obs}) and fecundity per capita of mature snails (f_{mat}) were derived from the results of capture-recapture surveys between summers 2013–14 and 2023–24 (Tables 5 & 6). The weighted mean for annual survival rate (S_{obs}) over the 9-year period is 0.524 (SD: 0.032; CI95%: 0.46 – 0.59) and the weighted mean of fecundity per capita of mature snails (≥ 30 mm diameter) present at the start of the interval between surveys (f_{mat}) is 0.475 (SD: 0.037; CI95%: 0.40 – 0.55).

Table 5. Estimates of annual survival rates (S_{obs}) for the intervals between capture-recapture surveys (Lloyd, 2024a) from capture-recapture analyses using Pradel's robust design model. Duration is the length of intervals between consecutive capture-recapture surveys in plots BCL01 and BCL02.

Plot	Duration	S_{obs}		
Interval	(Years)	Mean	SE	CI95%
BCL01				
15–16	2.016	0.432	0.083	(0.24 – 0.56)
17–18	1.603	0.501	0.095	(0.42 – 0.79)
19–20	2.041	0.631	0.070	(0.44 – 0.71)
21–23	2.984	0.666	0.084	(0.45 – 0.77)
BCL02				
15–16	1.918	0.309	0.069	(0.15 – 0.44)
17–18	1.605	0.613	0.120	(0.40 – 0.90)
19–20	2.041	0.560	0.078	(0.41 – 0.71)
21–23	2.984	0.448	0.099	(0.29 – 0.68)
Weighted mean of S_{obs}		Mean	SD	CI95%
		0.524	0.032	(0.46 – 0.59)

Table 6. Duration is the length of the intervals between consecutive capture-recapture surveys of the plots BCL01 and BCL02. P_{mat} is the proportion of mature snails (≥ 30 mm diameter) caught during surveys at the start of the intervals between surveys. Estimates of f_{obs} are the observed annual fecundity during intervals between capture-recapture surveys of plots BCL01 and BCL02 obtained from capture-recapture analyses using Pradel's robust design model. Estimates f_{mat} are fecundity per capita of mature snails (≥ 30 mm diameter) present at the start of the interval between surveys.

Plot: Interval	Duration (Years)	f_{obs}			P_{mat}			f_{mat}		
		Mean	SE	CI95%	Mean	SE	CI95%	Mean	SE	CI95%
BCL01										
15–16	2.016	0.234	0.048	(0.18 – 0.37)	0.784	0.028	(0.73 – 0.83)	0.299	0.062	(0.18 – 0.42)
17–18	1.603	0.376	0.104	(0.11 – 0.51)	0.747	0.046	(0.65 – 0.83)	0.504	0.143	(0.22 – 0.79)
19–20	2.041	0.170	0.068	(0.15 – 0.41)	0.541	0.043	(0.46 – 0.62)	0.313	0.127	(0.06 – 0.57)
21–23	2.984	0.209	0.045	(0.18 – 0.36)	0.658	0.045	(0.57 – 0.74)	0.318	0.072	(0.18 – 0.46)
BCL02										
15–16	1.918	0.272	0.050	(0.19 – 0.39)	0.694	0.031	(0.63 – 0.75)	0.392	0.074	(0.25 – 0.54)
17–18	1.605	0.331	0.079	(0.15 – 0.46)	0.659	0.050	(0.56 – 0.75)	0.502	0.125	(0.26 – 0.75)
19–20	2.041	0.293	0.031	(0.22 – 0.35)	0.398	0.042	(0.32 – 0.48)	0.737	0.111	(0.53 – 0.96)
21–23	2.984	0.299	0.035	(0.21 – 0.36)	0.423	0.047	(0.34 – 0.52)	0.705	0.113	(0.49 – 0.94)
Weighted mean of f_{mat} :								Mean	SD	CI95%
								0.475	0.037	(0.40 – 0.55)

The estimated weighted means for annual survival rate (S_{obs}) and fecundity per capita of mature snails (f_{mat}) together with the proportions of shells preyed on by weka, rodents and possums and the proportion with no evidence of predation by them (Table 2) were used to obtain additional demographic estimates by bootstrapping (Table 7). In the absence of density dependence (i.e., when population density is well below carrying capacity), the estimated λ_{nat} of 1.172 would result in annual population increases of 17% for snail population in the absence of the weka, rodents & possums.

Table 7. Parameter estimates from bootstrapping with standard deviation and the 2.5% & 97.5% quartiles of the bootstrapped values (CI95%). Parameter m_{pred} is the annual mortality rates for snails ≥ 20 mm diameter due to predation by weka, rodents or possum, while m_{nat} is the annual mortality rate for snails ≥ 20 mm diameter from all other causes. S_{nat} , f_{nat} and λ_{nat} are demographic parameter estimates for snail population in the absence of the weka, rodents & possums. S_{nat} is the annual rate of survival for snails ≥ 20 mm diameter, f_{nat} is annual fecundity per capita mature snails (≥ 30 mm diameter) and λ_{nat} is the annual rate of population increase.

	Parameter	Mean	SD	CI95%
With weka, rodents & possums	Mortality m_{pred}	0.346	0.031	(0.29 – 0.41)
	Mortality m_{nat}	0.275	0.029	(0.29 – 0.33)
Without weka, rodents & possums	Survival S_{nat}	0.725	0.030	(0.66 – 0.78)
	Fecundity f_{nat}	0.913	0.093	(0.75 – 1.11)
	Lambda λ_{nat}	1.172	0.042	(1.087 – 1.251)

Snail Population Trends With and Without Predators

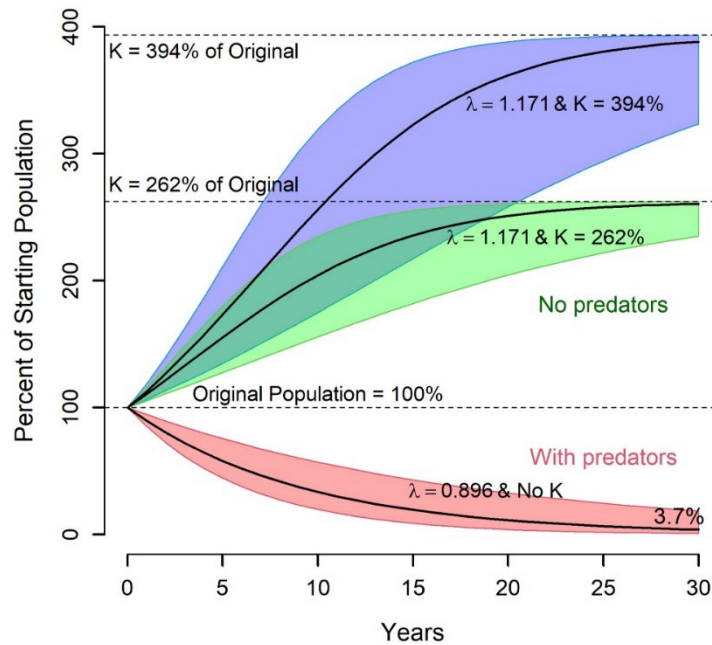
Snail population trends over a 30-year period were modelled using estimates of finite population increase (Table 8) with and without weka, rodents and possums (λ_{pred} and λ_{nat}). In the model of snail population trend in the presence of weka, rodents and possums (Figure 3 and Table 9), population estimates in models obtained using the mean estimate of λ_{pred} (0.8963) decline rapidly reaching one third of the starting population size within 10 years, approaching 10% of the starting population size after 20 years and 3.7% of the starting population size after 30 years. By contrast in models of snail population trends without weka, rodents and possums, using the mean estimate of λ_{nat} (1.1717), the snail populations increase rapidly, reaching more than twice the size of the starting population within 10 years and approach their carrying capacities (K_{lo} & K_{hi}) within 30 years.

Table 8. Lambda estimates for modelling snail population trends with and without weka, rodents & possums.

	Parameter	Mean	SD	LoCI 2.5% Quantile	UpCI 97.5% Quantile
With weka, rodents & possums	λ_{pred}	0.8963	0.0243	0.8498	0.9452
Without weka, rodents & possums	λ_{nat}	1.1717	0.0419	1.0865	1.2515

Table 9. Comparisons of the percentages of the initial population present at 5-year intervals in projected population trends for snail populations with and without predators and using high and low values of carrying capacity (K). Mean, LoCI and UpCI are population projections obtained using mean, and lower and upper CI95% values respectively of λ_{pred} and λ_{nat} .

N_0 1000	With Predators (λ_{pred})				Without Weka, Rodents and Possums (λ_{nat})							
	No K				$K_{lo} = 262\%$ of N_0				$K_{hi} = 394\%$ of N_0			
Yrs	λ_{pred}	Mean	LoCI	UpCI	λ_{nat}	Mean	LoCI	UpCI	λ_{nat}	Mean	LoCI	UpCI
5		57.8%	44.3%	75.5%		155%	128%	180%		173%	135%	211%
10		33.4%	19.6%	56.9%		204%	156%	235%		256%	175%	319%
15		19.3%	8.7%	43.0%		236%	182%	255%		323%	217%	372%
20		11.2%	3.9%	32.4%		251%	204%	261%		362%	258%	388%
25		6.5%	1.7%	24.5%		258%	222%	262%		380%	294%	392%
30		3.7%	0.8%	18.5%		261%	235%	262%		388%	324%	393%

Figure 3. Population trends for *P. patrickensis* with without the predators weka, rodents and possums and two values of carrying capacity, $K = 262\%$ & $K = 394\%$ of the original population. Black lines are population trends estimated using mean values for λ with and without predators (i.e., $\lambda_{pred} = 0.896$, & $\lambda_{pred} = 1.171$). The boundaries of the shaded areas are population trends estimated using upper and lower 95% confidence interval values for λ .

In Figure 3, the shaded areas are bounded by population trends modelled using the 2.5% and 97.5% confidence intervals around the mean estimates of λ (Table 8) and provide 95% confidence intervals around the population trends. In models of populations with predators (red shaded area), the lower bound of the confidence interval is only slightly lower than the population trend for the mean estimate of λ_{pred} reaching one fifth of the starting population size within 10 years, less than 4% of the after 20 years and 0.8% of the starting population size after 30 years (Table 9). The population trend at the upper bound of the confidence interval declines more slowly with 60% of the starting population size remaining after 10 years, 32% after 20 years and 18.5% of the starting population size after 30 years (Table 9). In models of populations without predators (green and blue shaded areas), population trends at the lower bound of the confidence intervals increase more slowly than population trend for the mean estimate of λ_{nat} and are 10% and 20% below carrying capacities after 30 years. Population trends at the upper bound of the confidence intervals increase rapidly, nearly doubling in 5 years and approaching carrying capacities within 20 years.

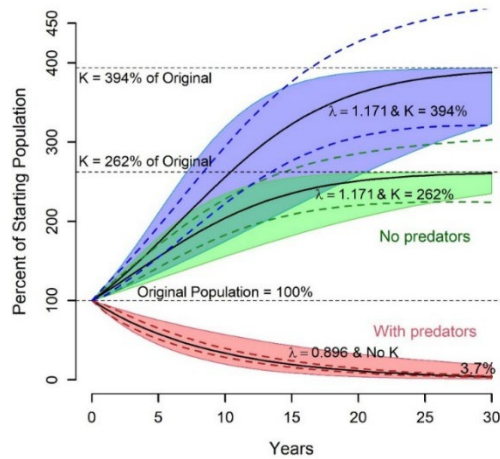


Figure 4. Population trends for *P. patrickensis* as described in Figure 3 with the lower and upper confidence intervals obtained by error propagation (coloured dashed lines) added for comparison.

Confidence intervals around population trends were also obtained by recursive implementation of logarithmic forms of the exponential and logistic population models with error propagation providing 95% confidence intervals around each population estimate (N_t). Figure 4 provides comparisons of confidence intervals from the two methods. The dashed coloured lines are lower and upper confidence intervals obtained by error propagation, while the shaded areas are bounded by confidence intervals obtained from population projections using the upper confidence intervals around mean estimates of λ as in Figure 3. The confidence intervals for population trends obtained from population projections using λ confidence intervals appear more credible than confidence intervals obtained by error propagation. In the density dependent models, population trends at the upper confidence intervals obtained by error propagation exceed carrying capacities by large margins, which seems unlikely. At population densities not near carrying capacities, confidence intervals obtained by error propagation are generally much narrower than those obtained from population projections using the confidence intervals around λ .

Population Projections With and Without the Project

Population trends in models of snail populations without the Project on the two plateaux (Figures 5 a–c & Tables 10 a & b) follow the same pattern as seen in the models with predators (Figure 3 & Table 9). Population trends for snail populations with the Project (Figures 5 a–c & Tables 10 a & b) combine annual population estimates for the fenced pest-free exclosures, calculated using λ_{nat} and the area of the exclosures available at the time, and annual estimates of population size in remaining undisturbed snail habitat outside of the pest-free exclosures calculated using λ_{pred} and the areas of remaining habitat at the time. Population trends within the pest-free exclosures follow the trajectories seen in models of snail populations without predators (Figure 3 and Table 9).

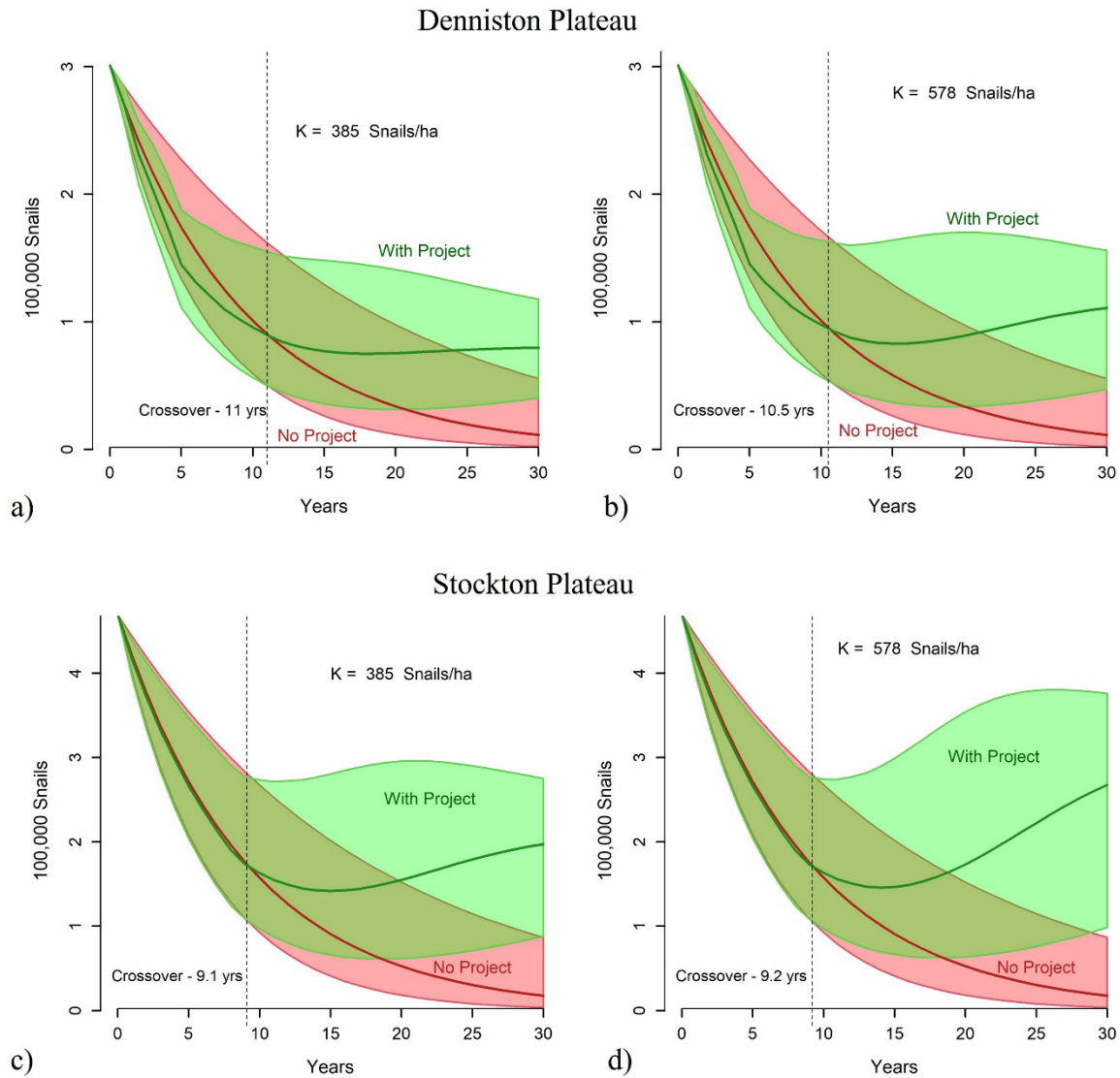


Figure 5. Models of snail population trends on (a & b) Denniston and (c & d) Stockton Plateaux with and without the Project, assuming (a & c) low carrying capacity, $K_{lo} = 385$ snails⁻¹ ha, and (b & d) high carrying capacity $K_{hi} = 578$ snails⁻¹ ha.

Table 10. Comparisons of the percentages of the initial population present at 5-year intervals in projected population trends for snail populations over a 30-year period on (a) Denniston & (b) Stockton Plateaux without the Project and with the Project and proposed pest-free fenced areas. Population trends were modelled with mean, lower and upper CI95% values of λ . Models with the Project were modelled with low and high values of carrying capacity (K_{lo} & K_{hi}) 385 and 578 snails⁻¹ ha.

a) Denniston $N_0 = 301,057$	Without Project (λ_{pred}) No K				With Project (λ_{nat})							
					$K_{lo} = 385$ snails ⁻¹ ha				$K_{hi} = 578$ snails ⁻¹ ha			
Yrs.	λ_{pred} :	Mean	LoCI	UpCI	λ_{nat} :	Mean	LoCI	UpCI	λ_{nat} :	Mean	LoCI	UpCI
5		58%	44%	75%		48%	37%	62%		48%	37%	63%
10		33%	20%	57%		32%	19%	53%		32%	19%	54%
15		19%	9%	43%		26%	12%	49%		28%	12%	54%
20		11%	4%	32%		25%	10%	47%		30%	11%	57%
25		6%	2%	24%		26%	11%	43%		34%	13%	55%
30		4%	1%	18%		26%	13%	39%		37%	16%	52%
N_{30} (Thousand)		11.27	2.28	55.57		79.70	40.15	117.7		110.9	47.16	155.9

b) Stockton $N_0 = 469,602$	Without Project (λ_{pred}) No K				With Project (λ_{nat})							
					$K_{lo} = 385$ snails ⁻¹ ha				$K_{hi} = 578$ snails ⁻¹ ha			
Yrs.	λ_{pred} :	Mean	LoCI	UpCI	λ_{nat} :	Mean	LoCI	UpCI	λ_{nat} :	Mean	LoCI	UpCI
5		58%	44%	75%		57%	43%	74%		57%	43%	74%
10		33%	20%	57%		35%	21%	58%		35%	21%	58%
15		19%	9%	43%		30%	14%	60%		31%	14%	64%
20		11%	4%	32%		33%	13%	63%		37%	14%	756%
25		6%	2%	24%		38%	15%	62%		47%	16%	81%
30		4%	1%	18%		42%	19%	59%		57%	21%	80%
N_{30} (Thousand)		17.57	3.56	86.68		197.4	88.11	275.1		267.6	98.31	376.1

In models of snail populations without the Project obtained using the mean estimate of λ_{pred} (0.8963), snail populations decline to around 11% of their initial size after 20 years and reach 3.7% of their initial size after 30 years on both plateaux. Populations on both plateaux declined more rapidly in models with the low estimate of λ_{pred} (0.8498), reaching 3.9% of their initial size after 20 years and 0.8% after 30 years. Conversely, populations declined more slowly in models with the high estimate of λ_{pred} (0.9452), only declining to 32% of their initial size after 20 years and 18% after 30 years.

In models with the Project and proposed fenced pest-free areas, during the first few years of the Project, the snail populations on both plateaux declined more rapidly than populations in models without the Project due to the loss of snail habitat to mining disturbance. The difference between population trends with and without the Project is larger for models of the snail population on Denniston Plateau (Figures 5 a & b) than Stockton Plateau (Figures 5 c & d), because a higher proportion of Denniston Plateau will be affected by mining. However, as the effects of the fenced pest-free exclosures manifest, with snail numbers increasing in the absence of predation by weka, rodents and possums, population declines in models with the Project

slowed until the modelled snail population sizes with the project equal and then exceed population levels in models without the Project. The cross-over point, when modelled snail populations with and without the Project are the same (Figures 5 a–d), ranging between 9 and 11 years after the Project began for all λ values and both carrying capacities (K). After reaching the crossover point snail populations in the fenced pest-free areas grow rapidly in the absence of predation by weka, rodents, and possums, while snail populations outside the pest-free enclosures continue to decline, primarily as a consequence of predation but also due to mining disturbance.

In models of snail populations on Denniston Plateau (Table 10 a) with the Project and pest-free enclosures obtained using the two values of carrying capacity ($K_{lo} = 385 \text{ snails}^{-1} \text{ ha}$ and $K_{hi} = 578 \text{ snails}^{-1} \text{ ha}$) and the mean estimate of λ_{nat} (1.1712), snail populations decline to around 25% & 30% of their initial size after 20 years and reach 27% & 37% of their initial size after 30 years. In models with the low estimate of λ_{nat} (1.0865), populations on Denniston Plateau were 10% & 11% of their initial size after 20 years and 13% and 16% after 30 years. In models with the high estimate of λ_{nat} (1.2515), populations on Denniston Plateau were 47% & 57% of their initial size after 20 years and 39% and 52% after 30 years.

Similarly, in models of snail populations on Stockton Plateau (Table 10 b) with the Project and pest-free enclosures obtained using the mean estimate of λ_{nat} (1.1712), snail populations decline to around 33% & 37% of their initial size after 20 years and reach 42% & 57% of their initial size after 30 years. In models with the low estimate of λ_{nat} (1.0865), populations on Stockton Plateau were 13% & 14% of their initial size after 20 years and 19% and 21% after 30 years. In models with the high estimate of λ_{nat} (1.2515), populations on Stockton Plateau were 63% & 76% of their initial size after 20 years and 59% and 80% after 30 years.

Table 11. Estimated numbers of snails inside and outside of fenced pest-free exclosures and the proportion of the snail populations inside the exclosures 30 years after mining starts in models with low and high values of the carrying capacity (K_{lo} & K_{hi}) and mean, lower and upper CI95% values of λ_{pred} outside the exclosures and λ_{nat} inside the exclosures.

			Values of λ_{nat}			Values of λ_{nat}		
			Mean	LoCI	UpCI	Mean	LoCI	UpCI
			1.172	1.087	1.252	1.172	1.087	1.252
Denniston Plateau			N_{30} Inside Fence ($K_{lo} = 385$):			N_{30} Inside Fence ($K_{hi} = 578$):		
			71,471	38,478	77,111	102,675	45,488	115,329
			<i>Proportion Inside Fence:</i>			<i>Proportion Inside Fence:</i>		
λ_{pred}	N_{30} Outside:		89.7%	82.4%	90.4%	92.6%	84.7%	93.3%
Mean 0.896	8,233		97.7%	95.8%	97.9%	98.4%	96.5%	98.6%
LoCI 0.850	1,669		63.8%	48.7%	65.5%	71.7%	52.8%	74.0%
UpCI 0.945	40,608							
Stockton Plateau			N_{30} Inside Fence ($K_{lo} = 385$)			N_{30} Inside Fence ($K_{hi} = 578$)		
			183,631	85,317	207,194	253,873	95,517	308,158
			<i>Proportion Inside Fence:</i>			<i>Proportion Inside Fence:</i>		
λ_{pred}	N_{30} Outside		93.0%	86.1%	93.8%	94.9%	87.4%	95.7%
Mean 0.896	13,766		98.5%	96.8%	98.7%	98.9%	97.2%	99.1%
LoCI 0.850	2,791		73.0%	55.7%	75.3%	78.9%	58.4%	81.9%
UpCI 0.945	67,903							

In models for snail populations with the Project, thirty years after the proposed Project begins most snails on both plateaux are in the pest-free exclosures (Table 11) for all combinations of the three values of λ_{pred} and λ_{nat} . In models for Denniston Plateau with mean values for λ_{pred} and λ_{nat} (0.896 & 1.1712) and the two carrying capacities ($K_{lo} = 385$ and $K_{hi} = 578$) 89.7% and 92.6% of the snail populations are inside the exclosure after 30 years. In models with low CI95% for λ_{pred} and upper CI95% for λ_{nat} 97.7% and 98.4% of the snail populations are inside the exclosure after 30 years, whereas in models with upper CI95% for λ_{pred} and lower CI95% for λ_{nat} 48.7% and 52.8% of the snail populations are inside the exclosure after 30 years. Results for Stockton Plateau show a similar pattern, in models with mean values for λ_{pred} and λ_{nat} and the two carrying capacities 93.0% and 94.9% of the snail populations are inside the exclosure after 30 years. In models with low CI95% for λ_{pred} and upper CI95% for λ_{nat} 98.7% and 99.1% of the snail populations are inside the exclosure after 30 years, whereas in models with upper CI95% for λ_{pred} and lower CI95% for λ_{nat} 55.7% and 58.4% of the snail populations are inside the exclosure after 30 years.

CONCLUSION

Predicted Population Trends

The models show that without significant conservation management interventions, *P. patrickensis* snail populations on the two plateaux will probably decline to 11% (range 3.9% to 32%) of their original population levels within 20 years and in most models, snail populations are at low levels 3.7% (range 0.8% to 18%) of their original population levels within 30 years (Figure 5 and Table 10), potentially approaching extinction without any impacts from the proposed Project.

Results from routine monitoring of snail numbers in a sample of 10 m square plots on Denniston Plateau undertaken for the Department of Conservation (DOC) between 2007 and 2021 provide independent confirmation of the results of these models. In the most recent ranking of the conservation status of *Powelliphanta* taxa, *P. patrickensis* is ranked as Nationally Critical because continuation of the high rates of decline observed in DOC's plots on Denniston Plateau would result in population declines of around 96% over the next three snail generations, or 30 years (Walker et al., 2024).

Although, stripping of snail habitat for the proposed Project will result in considerable reductions in the area of available habitat for the species on Buller Plateaux (Lloyd's Ecological Consulting, 2026) and initial reductions in size of the snail population, the models using the best estimate of λ_{nat} (i.e. mean $\lambda_{\text{nat}} = 1.1717$) indicate that the pest-free exclosures proposed as compensation for the Project's residual impacts on snails will reverse the snail population's decline within 15 years of the initial disturbance and result in stable or increasing, viable snail populations on the two plateaux within 30 years (Figures 5 a–d and Tables 10 & 11), albeit with lower numbers of snails than are currently present. In models using the lower 95% confidence interval value for λ_{nat} (i.e., 1.0865) snail populations begin to increase within 15 years of the initial disturbance and are still increasing 30 years after initial disturbance. The final population size 30 years after initial disturbance is as high or higher in models using the lower 95% confidence interval value for λ_{nat} than in models using the upper confidence interval value for λ_{pred} (i.e., 0.9452) in the absence of the Project.

The Reliability of the Snail Population Models

Before considering the reliability of the snail population models, it is worth reflecting on the role of modelling. The aphorism “*All models are wrong, but some are useful*” provides a valuable insight into the role of modelling. Essentially, models simplify the complexities of reality and are never entirely correct. However, well-constructed models can assist with decision-making about the real world.

The demographic data on *P. patrickensis* snail populations collected during capture-recapture surveys and Buller Plateaux wide snail-plot surveys (Lloyd, 2023, 2024a, 2024b) provide a rich source of demographic data. Ideally, population models should incorporate environmental

and demographic stochasticity, but the complexity of population models is constrained by available data and even simple models can provide useful insights (Morris & Doak., 2002). Obviously, the actual population trends will not follow the smooth trajectories seen in the models. The snail population models are based on the assumption that the population trajectory observed over the last 10 years is likely to continue into the future and consequently provides the best available forecast for the population's future trajectory. Using average demographic parameter estimate from the 9-year long capture-recapture study incorporates some environmental stochasticity into the models without adding unnecessary complexity. Expecting the population's recent past trajectory to continue into the future may prove wrong as a result of global climate change or unanticipated events such as disease or wildfires, but it is the best available information for developing models of future population trends.

There was no attempt to incorporate effects of climate change on *P. patrickensis* populations in the models because of the lack of reliable information on the topic. Walker et al. (2024) described the likely effects of climate change on *Powelliphanta* taxa as a combination of increased soil moisture deficits during summer resulting in desiccation of snails and increases in rat predation of snails as a result of warmer winters allowing expansion of ship rat's altitudinal range. Either of these effects could reduce survival and fecundity of *P. patrickensis*. Desiccation will have similar effects on *P. patrickensis* populations inside and outside of pest-free exclosures, whereas increased predation by rats will only affect *P. patrickensis* populations outside of pest-free exclosures. Consequently, negative effects of climate change on *P. patrickensis* are likely to be larger outside of the exclosures, increasing differences between population trends in models with and without the Project and associated pest-free exclosures.

Demographic Parameter Estimates

The demographic parameter estimates used to develop models of *P. patrickensis* populations subject to predation by weka and rodents are reliable estimates obtained directly from a capture-recapture study (Lloyd, 2024a). By comparison derivation of demographic parameter estimates for models of *P. patrickensis* populations without predation by weka and rodents is relatively intricate, leading to uncertainty over resulting parameter estimates for λ_{nat} .

The only comparable estimates of the annual finite rate of population increase (λ) in *Powelliphanta* snails are from two capture-recapture plots used to monitor populations of *P. hochstetteri* in Abel Tasman National Park (Lloyd et al., 2021). In one of the plots, predation by weka and rodents was rare during the four-year period 2016–2020, but predation by weka increased to high rates during the following year, 2020–2021. Annual finite rates of population increase in the plot were 1.26 and 1.20 during the 2016 – 2020 period without significant weka predation, but declined to 0.60 as weka predation surged. Thus, estimates of λ for a plot population of *P. hochstetteri* without significant predation by weka, rodents or possums are higher than our estimates of λ for *P. patrickensis* populations without predation by weka, rodents or possums (i.e., λ_{nat} in Table 8; Mean: 1.1717; CI95%: 1.0865 – 1.2515).

Published estimates of annual survival in *Powelliphanta* snail populations subject to relatively low levels of predation are similar to my estimate of 0.725 (CI95%: 0.66–0.78) for survival of *P. patrickensis* in the absence of weka, rodents and possum (S_{nat} in Table 7). The estimated annual survival for *P. patrickensis* in one plot in an area of VDT was 0.76 (CI: 0.5–0.95) during the period 2021–2024 (Lloyd, 2024c). Annual survival estimates for *P. patrickensis* in 4 plots of VDT ranged between 0.71 and 0.75 during the period 2010–2014 (MacKenzie, 2014). Annual survival estimates for *P. augusta* in 6 plots on the Mt Augusta ridgeline ranged between 0.66 and 0.82 during the period 2009–2020 (MacKenzie, 2014). Before high levels of predation by weka began in Abel Tasman National Park, the annual survival estimate for *P. hochstetteri* in one plot was 0.698 during 2016–2018 (Lloyd et al., 2021). The only comparable estimates of fecundity per capita adult are for *P. hochstetteri*, which ranged between 0.918 and 2.10 in two plots between 2016–2020 (Lloyd et al., 2021).

Parameter estimates in models for populations without predation by weka, rodents or possums are generally conservative, consequently population growth in the models is likely to be underestimated. There is no information on the rate of predation on small snails and eggs, which are likely to be consumed whole leaving no evidence of their predation. In the absence of other information, predation rate estimates for larger snails were used in models to estimate predation rates on small snails and eggs. These estimates are likely to underestimate actual predation on small snails and eggs, as they will be vulnerable to predation by mice as well as the predators of larger snails. Underestimating predation rates on small snails and eggs has no effect on models of populations with predation, because fecundity estimates are derived directly from the capture-recapture study, but underestimation will affect models without predation by weka, rodent or possums. In the latter models, fecundity estimates are derived using predation rate estimates, consequently underestimating predation rates on small snails and eggs will lead to underestimating fecundity, and hence underestimating population growth, in models without predation by weka, rodents or possums.

One exception to the tendency for parameter estimates being conservative may have occurred during bootstrapping. Factorial combinations of simulated values of S_{nat_i} , and f_{nat_i} used to estimate λ_{nat_i} during bootstrapping were assumed to be independent, without correlation. Correlation between survival (S) and fecundity (f) is likely in the real world, especially because in this study fecundity is defined as per capita recruitment rate of snails with diameters ≥ 20 mm per snail, and consequently includes the survival of smaller snails. Correlation between survival and fecundity will not affect mean estimates of λ_{nat} or the resulting population trends in the absence of predators, but could affect the width of confidence intervals lambda estimates and population trends. If survival and fecundity are positively correlated, the confidence intervals around lambda estimates and population trends will be underestimated, whereas if the two are negatively correlated, the confidence intervals will be overestimated. However, correlation between survival and fecundity was not apparent in the original results of the capture-recapture study, where Spearman's ρ statistic = 0.00. Any relationship between survival and fecundity is likely to be complex, affected by many variables such as environmental conditions, snail population densities, population age structure, disease prevalence and predation pressure.

Although there is no reliable information on density dependence in *P. patrickensis* populations, negative density-dependence is inevitable, with population growth rates declining as population density approaches the carrying capacity of the habitat. In the absence of better information, the highest snail population density observed in the past was used as a minimum estimate of carrying capacity ($K_{lo} = 385 \text{ snails}^{-1} \text{ ha}$), and a 50% higher value ($K_{hi} = 578 \text{ snails}^{-1} \text{ ha}$) was used to investigate how increasing carrying capacity estimates affected the models. In models with declining populations because of predation carrying capacities has no effect on the rate of decline in models. By contrast, in models without predation the value of the carrying capacity used in the model had a large effect, with increasing carrying capacities increasing both the rate of population growth and final population size. Models with the minimum carrying capacity estimate (K_{lo}) provide conservative estimates of population increase in the absence of predation.

Positive density dependence (i.e., Allee effects), where factors such as mate limitation or inbreeding depression, result in decreased rates of population growth at low densities (Courchamp et al., 2008; Kramer et al., 2009), were not incorporated into the models because there is no information on them. Including positive density dependence in models would result in increased rates of decline in models with populations depressed to low densities by predation by weka and rodents, but have no influence on models without predation.

Because of the complexity and unpredictability of the real world, it is unrealistic to expect that the population models described in this report will provide accurate descriptions of future trends in *P. patrickensis* snail populations on Buller Plateaux. However, the models provide useful insights into the likely fates of the snail populations with and without the Project and the proposed fenced pest-free exclosures.

APPENDICES

Appendix1: Parameter Estimates for Log-normal and Beta Distributed Variables

Demographic parameter estimates used in models of snail population trends have non-normal distributions. Fecundity, annual finite rate of population increase and population abundance are best described by log-normal distributions (Limpert et al., 2001), while survival, mortality and proportions are random variables with values between 0 and 1, best described by the beta distribution (Thompson Hobbs & Hooten, 2015). Error propagation and bootstrapping procedures used to develop the population models require parameter estimates for the distributions derived from the mean and variance or standard deviation of the variables using Equations 10 to 14, a & b.

The parameters describing a two-parameter log-normal distribution are the mean and standard deviation of the variable's natural logarithm (i.e., α_y and β_y), not the mean and standard deviation of the log-normal distributed variable itself (i.e., μ_x and σ_x). Equations 10 a & b were used to obtain estimates of the log-normal parameters (α_y and β_y) from the mean and standard deviation of the log-normal distributed variable (μ_x and σ_x).

$$\text{Equations 10 a \& b: } \alpha_y = \ln \left(\frac{\mu_x^2}{\sqrt{\mu_x^2 + \sigma_x^2}} \right) \text{ and } \beta_y = \sqrt{\ln \left(1 + \frac{\sigma_x^2}{\mu_x^2} \right)}$$

To reverse this procedure and obtain estimates of the mean and standard deviation of the log-normal distributed variable (μ_x and σ_x) from the log-normal parameters (α_y and β_y) Equations 11 a & b (Gelman & Hill, 2007) were used.

$$\text{Equations 11 a \& b: } \mu_x = e^{\left(\alpha_y + \beta_y^2/2\right)} \text{ and } \sigma_x = e^{\left(\alpha_y + \beta_y^2/2\right)} \times \sqrt{e^{\beta_y^2} - 1}$$

To get confidence intervals CI_y around α_y and CI_x around μ_x , Equations 12 a & b (Olsson, 2005) were used.

$$\text{Equations 12 a \& b: } CI_y = \alpha_y + \frac{\beta_y^2}{2} \pm z \sqrt{\frac{\beta_y^2}{n} + \frac{\beta_y^4}{2(n-1)}} \text{ and } CI_x = e^{(CI_y)}$$

Beta distribution parameters (θ and δ) were obtained from the mean (μ) and variance (σ^2) of a beta-distributed variable using Equations 13 a & b (Kruschke, 2011).

$$\text{Equations 13 a \& b: } \theta = \mu \left(\frac{\mu(1-\mu)}{\sigma^2} - 1 \right) \text{ and } \delta = (1 - \mu) \left(\frac{\mu}{\sigma^2} \right)$$

Equations 14 a & b (Thompson Hobbs & Hooten, 2015) were used to obtain the mean & variance (μ and σ^2) of a beta-distributed variable from the beta distribution parameters θ & δ .

$$\text{Equations 14 a \& b: } \mu = \frac{\theta}{(\theta + \delta)} \text{ and } \sigma^2 = \frac{\theta \delta}{((\theta + \delta)^2) \times (\theta + \delta + 1)}$$

Appendix 2: Using Lefkovitch Matrices To Estimate λ_{nat}

Deriving an estimate of lambda (λ) in the absence of predation by weka, rodents and possums (λ_{nat}) is complex and requires use of a stage-structured population projection matrix model. The model uses stage-dependent survival and fecundity estimates in Lefkovitch matrices (Lefkovitch, 1965) to project population growth rates. Four life stages were used to model population growth in *P. patrickensis*, with the expected or average duration of each of the stages derived from a growth curve obtained from repeated recaptures of individually tagged snails during the 9 years of the capture-recapture programme on Denniston Plateau (Lloyd, 2024a).

Stage 1 – $\geq 20 - 30$ mm: Age: $\geq 2 - 3.5$ yrs: Duration 1.5 yrs.

Stage 2 – $\geq 30 - 40$ mm: Age $\geq 3.5 - 8$ yrs: Duration 4.5 yrs.

Stage 3 – $\geq 40 - 41.5$ mm: Age $\geq 8 - 11$ yrs: Duration 3 yrs

Stage 4 – ≥ 41.5 mm: Age ≥ 11 : Duration 10 yrs.

Because snails < 20 mm diameter were not tagged during the capture-recapture programme, annual snail fecundity was defined as recruitment of snails with diameters ≥ 20 mm per reproductive snail (≥ 30 mm) in the previous year. Consequently, the life stage from eggs to 20 mm diameters snails, which takes *c.* 2 years, was represented by fecundity (f_{nat}) and not included as a separate stage in the population projection matrix.

In the Lefkovitch stage-structured population projection matrix, P_i is the probability of surviving and remaining in life stage i , G_i is proportion of the population in life stage i that grows into the next stage class and survives (i.e., the transition probability), and F_i is the annual fecundity of stage i (f_i). P_i , and G_i are calculated from the demographic estimates s_i , and d_i using Equations 15 and 16 (Carnia et al., 2015; Crouse DT, 1987; Yusoff, 2012), where s_i is the annual survival probability for stage i and d_i is the duration in years of stage i :

$$\text{Equation 15:} \quad P_i = \left(\frac{1 - s_i^{d_i-1}}{1 - s_i^{d_i}} \right) s_i$$

$$\text{Equation 16:} \quad G_i = \frac{P_i^{d_i}(1 - s_i)}{1 - s_i^{d_i}}$$

Although survival is likely to vary between the four life stages and fecundity is likely to vary between the three life stages after snails reach sexual maturity, there is no information on age-dependent variation, therefore the same values of S_{nat} and f_{nat} were used for s_i and f_i in all life stages. Estimates of S_{nat} and f_{nat} used in the Lefkovitch matrix were obtained by bootstrapping.

The stage-structured transition matrix model for *P. patrickensis* snails is a 4x4 square matrix with one column for each stage:

$$A = \begin{bmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix}$$

The population comprises individuals of four stage classes n_{1-4} , represented by the population vector (N):

$$N = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}$$

The population is projected through time using repeated matrix multiplication of the stage-structured transition matrix (A) and the population vector (Equation 17):

$$N_{t+1} = A \times N_t$$

or

$$\text{Equation 17: } \begin{bmatrix} n_{t+1} \\ n_{t+2} \\ n_{t+3} \\ n_{t+4} \end{bmatrix} = \begin{bmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix} \times \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}$$

Population projection was undertaken using the R-function *pop.projection* in the R-library *pobio* (Stubben & Milligan, 2007). The R-functions *lambda* and *stable.stage* were used to calculate the population growth rate of the projection matrix (λ) and the stable stage distribution of the projection matrix.

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